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SEASONAL PATTERNS IN A SAN FRANCISCO BAY, CALIFORNIA, SALT MARSH ARTHROPOD COMMUNITY

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Abstract.—Biomass, abundance, and species richness patterns of detritivore, herbivore, and carnivore components of a San Francisco Bay, California, salt marsh arthropod community were examined over an annual cycle. Abundance and species richness patterns for herbivores and detritivores did not track the occurrence of their respective food resources, perhaps because of the influence of salinity levels, and the frequency and duration of tidal inundation. In contrast, abundance and species richness of carnivores corresponded well with occurrence of their herbivore and detritivore prey, perhaps because carnivores are less susceptible to salt marsh environmental extremes. Trophic biomass analysis showed a typical pyramid-shaped relationship among producer, herbivore and detritivore, and carnivore components in spring; during autumn, however, the biomass of carnivores exceeded that of herbivores and detritivores.

Key Words.—salt marsh, wetlands, seasonality, trophic, arthropods, insects, *Salicornia*

Over an annual cycle, salt marshes are subject to relatively large seasonal fluctuations in tidal inundation frequency and duration, and in soil, ground water, and tidal water salinity. Does the composition of the arthropod fauna show similar temporal fluctuations? If all species of salt marsh arthropods are well adapted to the full range of tidal inundation and salinity that occurs over a year, the occurrence of a trophic group and the availability of its food resources should correspond, as has been reported for more seasonally constant environments (e.g., Hurd & Wolf 1974, Brown & Southwood 1983). However, if physical conditions disrupt the ability of a trophic group to track its food resources, poor correspondence may result. In this paper, we describe the seasonal occurrence of arthropods (as measured by biomass, abundance, and number of species), and relate these findings to the above considerations.

Materials and Methods

The study was conducted in Petaluma Marsh, Sonoma Co., California (for map of area, see Balling & Resh 1983: Fig. 1), which is the largest of the San Francisco Bay tidal marshes and one of the largest (1145 ha) estuarine marshes along the Pacific Coast of North America. The marsh is dominated by pickleweed (*Salicornia virginica* L.).

Arthropods were collected using a D-vac suction device with a 0.25 mm mesh collection bag, and were separated from plant matter using a Berlese-Tullgren funnel; a complete description of arthropod sampling methods is given in Balling & Resh (1982). Samples for the present analysis were chosen from a series that was taken approximately monthly from January to November 1978 (representing 12 sampling dates). Specimens were separated into three categories: detritivores, herbivores, and carnivores. Primary feeding habits of the species were obtained from taxonomic specialists in these groups and from existing literature (e.g., Cameron 1972). Although some species do not feed restrictively within a single trophic group, we used the predominant feeding mode of a species to describe its trophic status.

Arthropod abundance and species richness (number of species per 0.09 m^2 sample) were based on data from six samples collected each month. Arthropod biomass was determined from two samples each month, which were individually oven dried at 100° C to a constant weight.

Detailed measurements of physical variables (salinity, tidal inundation, and air temperature) were not done in Petaluma Marsh until 1980; however, values during that year matched periodic observations made during 1977–1979. In 1980, salinity of tidal waters was measured weekly (during high tide) with a refractometer; periodic measurements of interstitial water salinity (Balling & Resh 1983) indicated similar seasonal trends observed to those for tidal water salinity. Tidal inundation frequency of the marsh surface was calculated using data from a tide gauge located on a nearby slough. Average air temperature was determined from constant temperature recordings.

Results and Discussion

Biomass.—Arthropod biomass during the year was characterized by three narrow, well-defined peaks; each peak represented a different trophic level: detritivores peaked in March, herbivores in May and June, and carnivores in September and October (Fig. 1a). At least in part, these biomass patterns reflected the phenology of the large sized species in the arthropod community. For example, the peak in detritivores closely followed peak occurrences of the amphipod *Orchestia traskiana* Stimpson and the isopod *Littorophiloscia richardsonae* (Holmes & Gay). Herbivores were not dominated by any single species; instead the peak largely resulted from four species of brine flies [Ephydridae: *Psilopa* (*Ceropsilopa*) *coquilletti* (Cresson), *Scatella* (*Scatella*) *stagnalis* Fallen, *Scatella* (*Neoscatella*) *setosa* Coquillett and *Scatophila* sp.] and two species of leafhoppers [Cicadellidae: *Streptanus confinus* (Reuter) and *Macrosteles* sp. near *fascifrons* (Stål)]. The carnivore peak reflected the maturation of the population of the large wolfspider (Lycosidae) *Pardosa ramulosa* (McCook).

Abundance.—Of all trophic groups, more individuals of carnivores than herbivores or detritivores were collected throughout the year; however, the abundance peaks were less well defined than the biomass peaks (Fig. 1b). Abundance of all groups peaked in spring and then again in autumn. In contrast to the influence of large individuals on biomass, changes in abundance are often biased toward the smaller sized, more numerous species (e.g., Odum 1971). For example, the spring detritivore peak was dominated by the sminthurid collembolan *Sminthurides* (*Sminthurides*) *malmgreni* Tullberg and the autumn peak was dominated by the psocopteran *Lachesilla pacifica* Chapman. The spring peak in herbivores was dominated by the same species of brine flies and leafhoppers as the herbivore biomass peak. However, the earlier rise in abundance seen in March was caused by early instar leafhoppers, whose small size made them proportionately more important in abundance measures than in biomass measures. Carnivore abundance peaks in spring and autumn were dominated by the small predaceous phytosieid mite *Amblyseius scyphus* Schuster & Pritchard, and also included a broad array of other mites and spiders.

Species Richness.—Like abundance, the peaks in species richness were less well

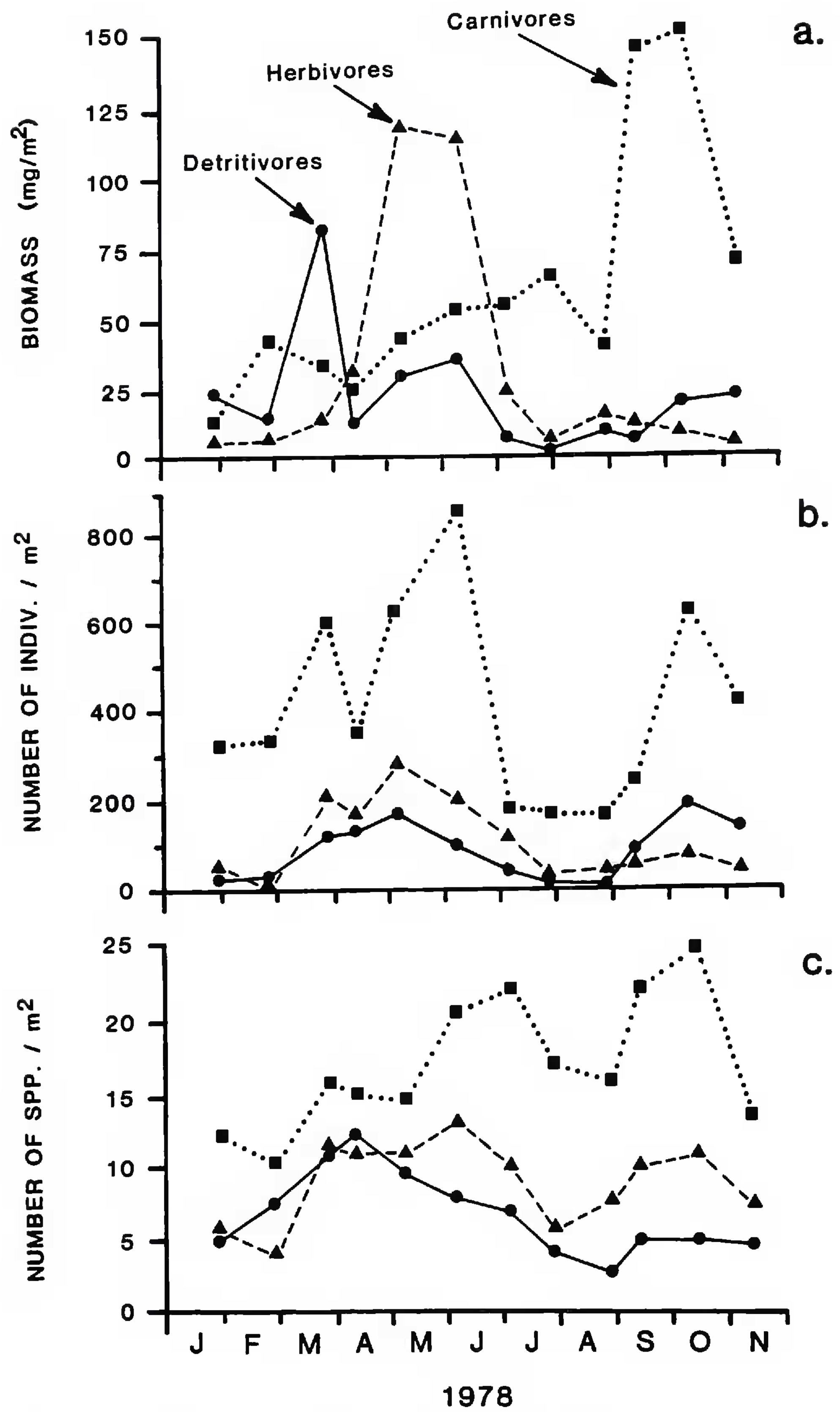

Figure 1. Mean (a) biomass, (b) abundance, and (c) species richness of terrestrial arthropods collected in Petaluma Marsh during 1979; squares represent carnivores, triangles represent herbivores, and circles represent detritivores.

defined than those for biomass. Detritivore species richness was highest in April, with only a small increase in autumn. Herbivore species richness was highest in June (although this was preceded by similarly high levels that began in March), decreased in July and August, and increased again in September and October. Carnivore species richness peaked in May, June and July, and October.

Trophic Pyramids.—Because biomass relationships among different trophic groups changed seasonally (Fig. 1a), the shape of ecological pyramids that are developed from biomass data vary depending on the time of year. For example,

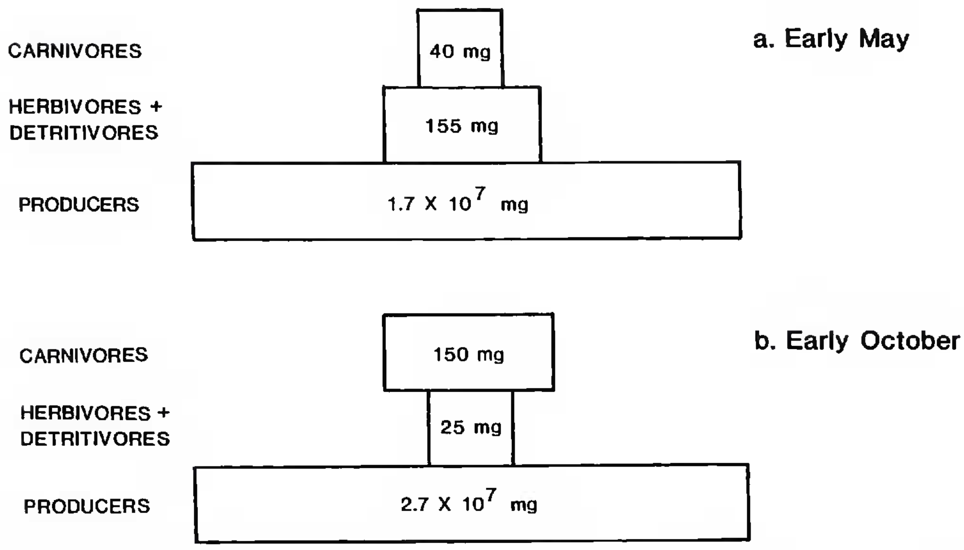

Figure 2. Trophic pyramids of pickleweed and arthropod biomass in (a) early May and (b) early October 1979. Plant biomass data are from Cameron (1972) and Balling & Resh (1983). Pyramid widths are given as the $\log_{10}$ of the biomass (mg/m^2).

during early May the trophic relationships were pyramid shaped; biomass estimates of producers (pickleweed), herbivores/detritivores (combined to estimate potential carnivore prey), and carnivores decreased at successively higher trophic levels (Fig. 2a). In contrast, during early October the carnivore and herbivore/detritivore relationship was inverted (Fig. 2b).

Interaction of Trophic Groups and Abiotic Factors.—Although biomass patterns in this salt marsh arthropod community showed seasonal changes indicating trophic succession, the abundance and species richness patterns showed neither trophic succession nor the typical numerical domination of herbivores. Perhaps this is related to the seasonal patterns of physical features of the salt marsh environment.

In Petaluma Marsh, water salinities were lowest in February, March, and April; they steadily increased through the following summer, and then decreased with the onset of rain at the beginning of the wet season in October (Fig. 3a). Tidal inundation frequency (Fig. 3b) and air temperature (Fig. 3c) showed similar patterns.

Detritivores had their highest biomass, abundance, and species richness during spring, even though their primary food resource (which in a pickleweed monoculture is composed of litter from senescent stems) was most abundant in October and November (Cameron 1972). The early spring flushing of the marsh surface by rainfall and low salinity tides reduces the salt content of surface litter, which may make it more palatable to insect detritivores (Foster & Treherne 1976). In addition, microbial colonization may condition the litter by this time, which also provides bacterial and fungal food sources.

Abundance, richness, and biomass of detritivores declined gradually until August, even though abundant litter still occurred in the marsh; perhaps this decline resulted from high salinities of tidal water (over 20 ppt, Fig. 3a) and frequent tidal inundation of the marsh (Fig. 3b). During July and August, the marsh surface is inundated by tides approximately 10% of the time and for periods of up to 5.5 h. Such inundations are stressful to arthropods that remain under water, and also to those that remain on the water surface or migrate to the tops of emergent

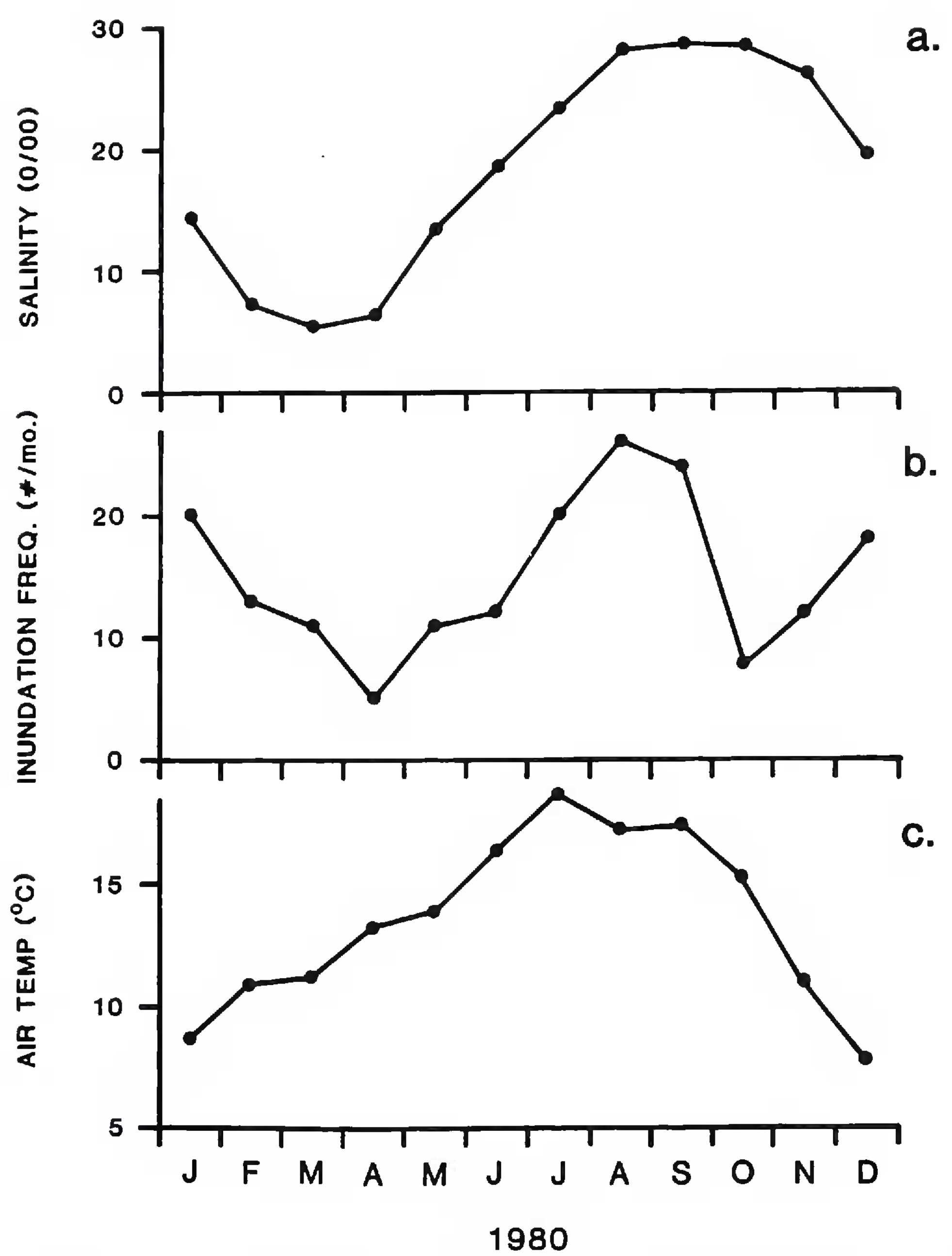

Figure 3. (a) Mean salinity of tidal water, (b) frequency of tidal inundation (per month), and (c) mean maximum air temperature in Petaluma Marsh during 1980.

vegetation because they will be more susceptible to predation or washout by receding tides (Foster & Treherne 1976).

In autumn, the psocid *L. pacifica* was the only detritivore to increase in abundance. The apparent salt tolerance of this species allows it to use this abundant food source at a time when few other detritivore species are present (e.g., Fig. 1c shows an average of only four detritivore species per sample during September and October).

Abundance and biomass of herbivores is highest in late spring even though their food, which consists mostly of surface algae and the annual succulent component of pickleweed, increases in quantity from March through October (Cameron 1972, Mahall & Park 1976, Zedler 1982, Josselyn 1983). The rise in herbivores coincides with the most rapid increase in succulent plant biomass, and with the seasonal increase in air temperature (Fig. 3c). The rather sudden decline coincides with the combination of peak tidal inundation (Fig. 3b) and peak salinities (Fig. 3a).

Tidal salinities, which correlate with groundwater salinities, indirectly affect sap-feeders such as leafhoppers through reductions in their food quality because pickleweed sap salinity increases as groundwater salinity increases (Flowers et al. 1977). For example, Regge (1973) has shown that salt marsh aphids will seek plants with lower sap salinity, and Vince et al. (1981) have shown that a positive relationship between *Spartina* nutritional quality and herbivore abundance occurs in an Atlantic coast salt marsh.

The decline of herbivores at the end of spring also coincided with the rise in carnivore abundance; thus, predation may also be an important regulating factor. Again, as with the detritivores, high tides of mid-summer may drive some insects to the plant tops or water surface, and thus increase the chances of predation. Vince et al. (1981) also indicated that spider predation may limit herbivore abundance.

The seasonal patterns of carnivore abundance and species richness corresponded well with the occurrence of expected food sources (i.e., herbivores and detritivores). Carnivores, represented primarily by mites, reached their peak abundance in spring, which coincided with the herbivore and detritivore abundance peaks. Although carnivore abundance declined through the summer, biomass continued to rise. Most of the autumn predators are spiders that are well adapted to traversing water surfaces and capturing prey that are found there (Roth & Brown 1976). Because most of their prey regulate the salinity of their hemolymph (at least to some extent), predators may be less affected by the rise in salinities during summer and autumn.

In conclusion, salt marsh herbivores and detritivores apparently do not closely track changes in the quantity of their food. In fact, the inefficiency of the detritivores may help promote the rapid accumulation of peat that occurs in many salt marshes. The results of this study suggest that the phenologies of salt marsh herbivores and carnivores are determined less by the quantity of food than by tidal inundation and the quality of food, which in turn is affected by tidal and groundwater salinities (Collins et al. 1986, Collins & Resh 1989). Carnivores, in contrast, appear to respond to food availability rather than to the physical extremes of the salt marsh environment.

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